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THE DISTRIBUTION OF THE BRYOPHYTES AND VASCULAR PLANTS WITHIN LITTLE DOLLAR LAKE PEATLAND, MACKINAC COUNTY, MICHIGAN

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ABSTRACT. Little Dollar Lake peatland, a *Sphagnum*-dominated poor fen peatland complex, has a flora consisting of 36 bryophyte and 93 vascular plant species. Random, quantitative sampling of 279 one-meter-square quadrats along 13 transects on six peatland mats was analyzed by two-way indicator species analysis (TWINSPAN). Based on interpretation of the TWINSPAN analysis, three vegetation cover types and six constituent vegetation phases were delineated. The three cover types were designated as the *Calamagrostis canadensis* cover type (lagg habitats), the *Chamaedaphne calyculata* cover type (peatland mat habitats), and the *Chamaedaphne calyculata–Triadenum fraseri* cover type (transitional habitats with evidence of terrestrialization). A fourth association, the *Potamogeton confervoides–Utricularia geminiscapa* cover type, was recognized based on qualitative field observations and consisted of the aquatic vegetation within Little Dollar Lake. Botanical evidence suggests that terrestrialization and small-scale paludification are occurring in some areas of the peatland.

Key Words: peatland, bog, fen, *Sphagnum*, bryophytes, vascular plants, terrestrialization, TWINSPAN, Michigan

Peatlands are wetlands especially characteristic of northern regions across North America and Eurasia that form in cool, temperate or maritime climates where evapotranspiration is low. Peat deposits dominate the boreal environments of Canada (170 × 10^6 ha), the former Soviet Union (150 × 10^6 ha), and the United States (36.8 × 10^6 ha; Gorham 1990). Near the southern edge of the glacial boundary in North America, peatlands tend to be more sporadic and are usually confined to smaller areas (typically glacial scour basins or kettleholes), as opposed to the extensive mires that blanket the landscape of subarctic latitudes (Crum 1988). Along the glacial boundary, peatland basins are frequently frost pockets that serve as refugia for northern plants at the southern edge of their ranges (e.g. Andreas and Bryan 1990; Crum 1988; Damman and French 1987; Pielou 1979).

The peat of boreal regions consists of partially decomposed remains of bryophytes (especially *Sphagnum*) and vascular plants (primarily sedges and ericaceous shrubs), as well as minute amounts of inorganic matter (Crum 1988; Damman and French 1987; Moore and Bellamy 1974). Although the majority of wetlands produce peat to some extent, northern peatlands store vast quantities of peat because rates of organic deposition greatly exceed rates of decomposition (Crum 1988).

Peatlands are typically associated with acidic water chemistry. The main causes of peatland acidity are the result of a variety of biogeochemical processes and positive feedbacks (Crum 1988; Gorham 1957; van Breeman 1995) involving the presence of organic acids within the anoxic subsurface peat (Hemond 1980; Kilham 1982), the high cation exchange capabilities of *Sphagnum* taxa (Andrus 1986; Clymo 1963, 1964; Crum 1988; Kilham 1982; Spearing 1972; Vitt et al. 1975), the uptake of ions by vegetation (Kilham 1982), the overall hydrological characteristics of individual peatland systems (Kilham 1982; Vitt et al. 1975), the oxidation of reduced sulfur compounds (Clymo 1964; Gorham 1961), and, occasionally, acid precipitation (Clymo 1964; Crum 1988).

Conditions within peatlands are generally considered less than optimal for vascular plant growth and establishment (Clymo and Hayward 1982; Moore and Bellamy 1974; van Breeman 1995; Vitt et al. 1995). However, extensive bryophyte communities thrive in peatland environments of boreal landscapes (Vitt 1990). Due to their intimate contact with the aqueous chemical environment of the peatland, bryophytes are strong indicators of microhabitat conditions (Vitt and Slack 1984). Peatland vegetation distributes itself based largely on gradients of minerotrophy (e.g. alkalinity) and pH, as well as light and hydric conditions of microhabitats (e.g. Anderson and Davis 1997; Gignac and Vitt 1994; Jeglum 1971; Vitt and Chee 1990; Vitt and Slack 1975; Wheeler et al. 1983).

Peatlands exhibit strong floristic similarities across much of North America, resulting in similar species composition patterns in regions such as the Northeast and upper Midwest of North America (Crum 1988; Gore 1983; Wheeler et al. 1983). From site to site, the diversity of both bryophyte and vascular peatland floras is highly influenced by the microhabitat heterogeneity of the peatland. The greater the diversity of microhabitats available, the greater the species richness of the peatland (Anderson and Davis 1997; Vitt et al. 1995).

An extensive and often confounding literature exists regarding the classification of peatland systems. Researchers classify peatlands utilizing a variety of terms and definitions that assess peatland attributes ranging from edaphic and physical characteristics to vegetation community composition (Gore 1983). Based on water chemistry, peatlands can be classified generally into two polar groups, ombrotrophic peatlands (bogs) and minerotrophic peatlands (fens). A third group, oligotrophic peatlands, have intermediate water chemistry and floristic characteristics.

Ombrotrophic peatlands receive all mineral subsidies from atmospheric deposition or from nutrients released during the slow decay of organic matter within the peatland basin. Thus, these peatlands are extremely nutrient-limited (Crum 1988; Damman and French 1987; Gore 1983). Ombrotrophic peatlands may be cut off from drainage or flushing by their geomorphological orientation, such as in a kettlehole bog. These peatlands may also be isolated from the water table by their own prolific deposition of peat that can elevate the peatland above the influence of groundwater, such as in a maritime raised bog (Crum 1988; Damman and French 1987). Due to the lack of active water circulation, hydrogen ions accumulate in ombrotrophic peatlands often resulting in pH values of 4.01–4.25 in the narrow definition of Gorham and Janssens (1992a), or less than 5.0 in the broader definition of Vitt et al. (1995). Bryophyte communities in ombrotrophic and oligotrophic peatlands are extensive and are dominated by *Sphagnum* species (Crum 1988; Gorham and Janssens 1992a; Janssens and Glaser 1986; Schwintzer 1981; Vitt 1990, Vitt and Slack 1975, 1984; Vitt et al. 1995).

Minerotrophic peatlands (fens) are relatively nutrient-rich compared to their ombrotrophic counterparts. Fens receive mineral subsidies from rheotrophic (flowing) ground or surface sources, as well as from precipitation. The nutritive input of a fen is unique from site to site based on the physical orientation and hydrology of the peatland. Thus, the mineral concentrations of fens are tremendously variable (Damman and French 1987; Gignac and Vitt 1994; Gore 1983). Edaphic inputs enrich fen peats with higher concentrations of calcium, iron, magnesium, aluminum, and phosphorus ions and higher relative pH levels than ombrotrophic peatlands (Gignac and Vitt 1994; Gorham 1990;

Jeglum 1971; Schwintzer 1978; van Breeman 1995). Fens are often subclassified as poor fens (pH 4–6) to extreme rich fens (pH 6–7.5) based on the relative minerotrophy, pH values, and plant species composition (pH values for the upper Midwest from Crum 1988).

The relative minerotrophy and higher pH levels of fens are reflected in their floras which become more species-rich along a gradient from low to high nutrient availability, i.e., oligotrophic to minerotrophic conditions (Crum 1988; Damman and French 1987; Glaser 1987; Gorham 1990; Schwintzer 1981). Fens typically have an extensive sedge cover that is often dominated by *Carex lasiocarpa* Ehrh., a less prominent bryophyte cover, and greater overall species richness compared to ombrotrophic peatlands (Crum 1988; Glaser 1987; Schwintzer 1978; Vitt et al. 1995).

Bryophytes in fens tend to be dominated by members of the Amblystegiaceae, including *Amblystegium* spp., *Calliergon* spp., and *Scorpidium scorpioides* (Hedw.) Limpr. (Gorham and Janssens 1992a; Janssens and Glaser 1986; Vitt 1990; Vitt et al. 1995). *Sphagnum* taxa have reduced frequencies in fen ecosystems, but are nevertheless present. Species such as *Sphagnum teres* (Schimp.) Ångstr. ex C. Hartm. and *Sphagnum subsecundum* Nees ex Sturm are typically prominent in alkaline fen conditions, particularly on the edge of the mat along open water (Crum 1988).

Most basin peatlands containing ponds or lakes exhibit the classic zonation of vegetation communities where a floating community of sedges, *Sphagnum,* and/or ericaceous shrubs encroach over the open water of a lake (e.g., Crow 1969; Dunlop 1987; Fahey 1993; Fahey and Crow 1995; Schwintzer and Williams 1974). The more or less concentric vegetation patterns of peatlands that radiate outward from lake margins led early ecologists to propose the "hydrosere model" of peatland succession. The hydrosere model states that lake margin communities fill in or terrestrialize the open water of a pond or lake, and initiate a successional sequence that passes through ericaceous shrub associations, coniferous forest associations, and finally culminates in an upland forest climax community on what was formerly the peatland (e.g., Dansereau and Segadas-Vianna 1952; Gates 1942; Transeau 1903).

Recently, this traditional hydrosere explanation that links spatial zonation with successional processes has been called into question by peatland ecologists (Klinger 1996; van Breeman 1995). Although the process of terrestrialization in basin peatlands has been well documented, Klinger (1996) has reservations regarding two major tenets of the hydrosere model. First, it is unlikely that a mesic forest "climax" is the ultimate successional destiny of a peatland basin. Second, terrestrialization of peatlands is not necessarily a unidirectional process; instead it is quite often a dynamic progression of vegetation advance and recession along a water body (e.g. Schwintzer and Williams 1974).

Citing a lack of data from stratigraphic, dendrochronological, and vegetational analyses to support strict hydrosere peatland succession, "the bog climax model" of peatland succession has been proposed (Klinger 1996). This model states that peatland conditions are their own climax in middle to high latitudes. In this model, peatland mats extend outward from lake margins via terrestrialization, while *Sphagnum* mosses along the outer edge of the peatland expand beyond the limits of the basin and into the upland via paludification. Therefore, in the absence of large scale disturbances and alterations of peatland hydrology, peatland systems remain ecologically intact for thousands of years (Klinger 1996). Early in peatland succession allogenic factors are important, but they later become secondary to autogenic factors that are initiated and maintained by the flora itself (Klinger 1996).

This paper outlines the vegetation associations found within Little Dollar Lake peatland based on field observations and TWINSPAN analysis. Comparisons of vegetation patterns at Little Dollar Lake peatland to other North American peatlands in the upper Midwest, Canada, and the Northeast are emphasized. The role of terrestrialization and paludification in peatland succession is also discussed with reference to vegetation patterns observed at Little Dollar Lake peatland.

SITE DESCRIPTION

The Little Dollar Lake peatland basin is 14 hectares (34 acres) in area. The peatand is located in west-central Mackinac County on the eastern Upper Peninsula of Michigan (T44N, R8W, NE1/4 Sec. 28, Hudson Township). Little Dollar Lake has acidic water chemistry (mean pH = 4.5, n = 40) and is situated in a shallow glacial scour basin. Based on pollen stratigraphy and sedimenta-

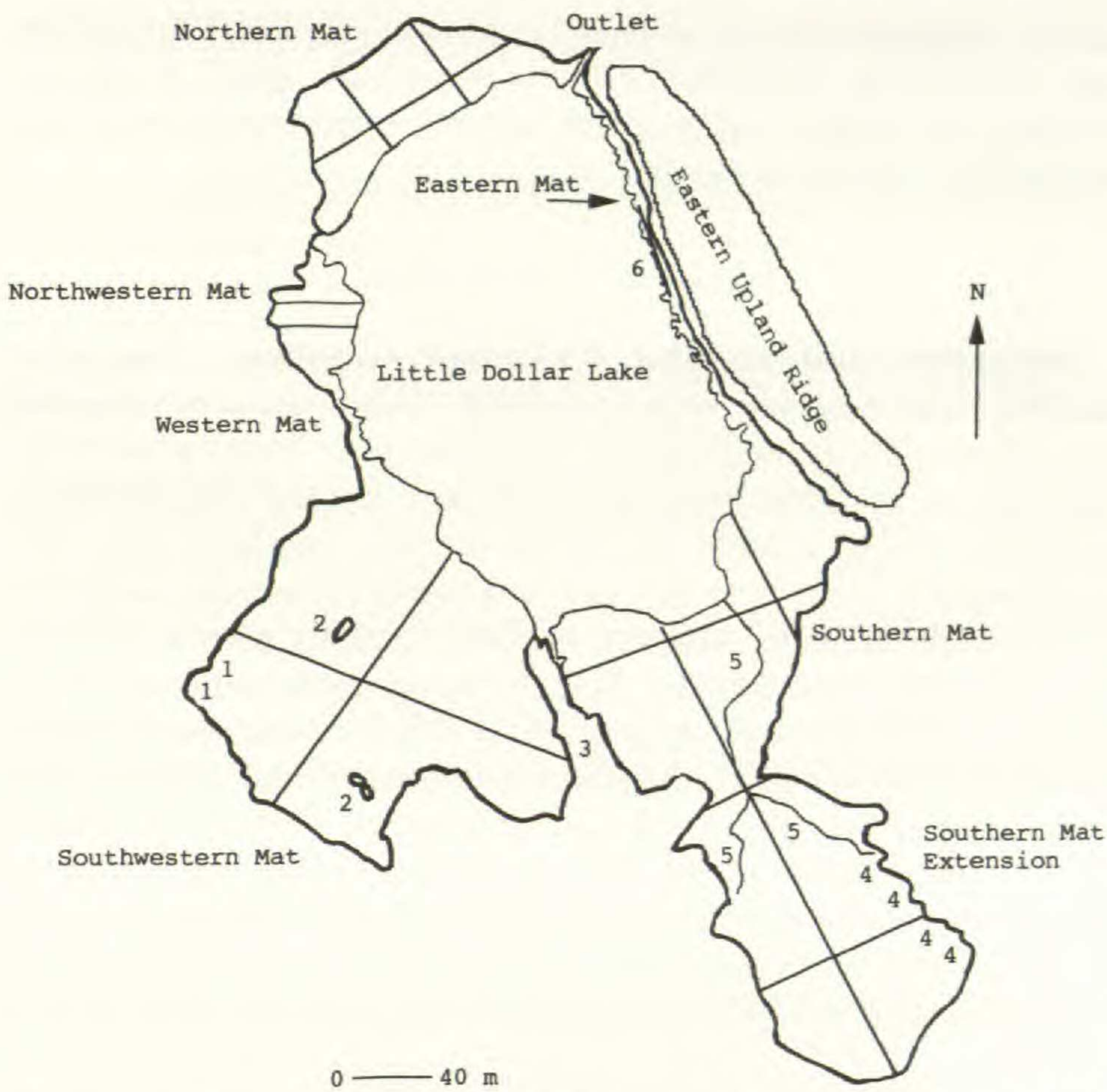

Figure 1. Map of Little Dollar Lake peatland illustrating transect locations and selected features of local geography around and within the peatland basin. Scale is approximate. 1. *Typha* colony adjacent to the truck trail; 2. Upland islands on southwestern mat; 3. Upland peninsula; 4. Muck pools in the southern mat extension; 5. Stream channel; 6. Location of the transect on the eastern mat parallel to the upland.

tion, the peatland around Little Dollar Lake began to form approximately 3500 years before present as a result of prolonged increases in the regional water tables of eastern upper Michigan (Futyma 1982). Basin morphology, post-glacial history, soils, surrounding upland vegetation, and climate are described by Hellquist (1996) and Hellquist and Crow (1997).

Little Dollar Lake is surrounded by seven peatland mats of varying extent. These mats were named based on their compass-point position around Little Dollar Lake (Figure 1). Each mat is colonized by a variety of plant associations. In general, the peatland is characterized by a nearly continuous layer of *Sphagnum* spp. covered by expanses of open ericaceous scrub. A narrow, floating mat fringes much of the lakeshore and a graminoid lagg borders the upland of several mats.

MATERIALS AND METHODS

Bryophyte and vascular vegetation sampling. Vegetation analysis and mapping were conducted using transect sampling procedures. Thirteen transects, intersecting as many plant communities as possible, were surveyed and divided into ten-meter intervals. Using a table of pseudo-random numbers, two one-meter-square (1 m × 1 m) quadrats were chosen for sampling within each ten-meter interval. In some spatially narrow habitats, extra quadrats were added to help insure adequate sampling. From July 12, 1995 through August 15, 1995, 279 one-meter-square quadrats were sampled visually for frequency and absolute percent cover of bryophyte and vascular species. Cover was defined as "... an estimate of the area of coverage of the foliage of the species in a vertical projection on to the ground" (Shimwell 1971, p. 110). Species composition and absolute percent cover were estimated separately for the bryophyte and vascular strata in each quadrat.

TWINSPAN vegetation analysis. Bryophyte and vascular percent cover data from the 279 sampled quadrats were analyzed using two-way indicator species analysis (TWINSPAN; Hill 1979). TWINSPAN is a polythetic divisive procedure that uses reciprocal averaging to ordinate quadrats, ultimately creating an ordered site-by-species two-way table (Hill 1979). Seven pseudospecies cut levels (Hill 1979; van Tongeraan 1987) were established as follows: 1 (0–1% cover), 2 (1–2% cover), 3 (2–5% cover), 4 (5–10% cover), 5 (10–25% cover), 6 (25–50% cover), and 7 (50–100% cover). All cut levels were weighted equally.

For studies involving the classification of ecological communities, there are several advantages to employing TWINSPAN analysis. These include its use of raw data, its hierarchical classification of both plots and species, and the ability to rewrite the arranged data matrix in a dendrogram format that enhances the clarity of plot relationships (Gauch 1982). TWINSPAN analysis has been utilized in many investigations of peatland vegetation

Table 1. Species richness of the four vegetation cover types (CT) and six cover phases (PHS). The number of quadrats in each cover type or phase is noted in parentheses.

TWINSPAN Community Delineation	Species Richness
Potamogeton confervoides–Utricularia geminiscapa CT	7
Calamagrostis canadensis CT (27)	54
Iris versicolor–Lycopus uniflorus PHS (13)	44
Sphagnum cuspidatum–Dulichium arundinaceum PHS (14)	30
Chamaedaphne calyculata CT (220)	56
Sphagnum recurvum–Carex oligosperma PHS (186)	53
Sphagnum magellanicum–Sarracenia purpurea PHS (34)	27
Chamaedaphne calyculata–Triadenum fraseri CT (32)	37
Sphagnum majus PHS (22)	26
Sphagnum papillosum PHS (10)	31

(Anderson and Davis 1997; Dunlop 1987; Fahey and Crow 1995; Miller 1996; Slack et al. 1980; Vitt and Chee 1990; Vitt et al. 1990).

RESULTS

TWINSPAN classification. Field observations and data weighed in concert with TWINSPAN analysis resulted in the delineation of four distinct vegetation cover types (including the aquatic vegetation of the lake) and six constituent vegetation phases within the Little Dollar Lake basin (Table 1; Figures 2 and 3). The aquatic cover type was recognized based on field observations. Although these cover types were delineated primarily through TWINSPAN analysis, only plant communities that could be discerned clearly in the field have been recognized. The complete TWINSPAN two-way table and raw data are available in Hellquist (1996).

Those species that were prominent both in the field and in the TWINSPAN analysis were chosen as appropriate species to name the cover types (CT) and phases (PHS). Due to overlap of indicator species between clusters, or to the relatively inconspicuous nature of the TWINSPAN indicator species in the physiognomy of a cover type or phase, the TWINSPAN indicator species were not always adopted as appropriate "representative species" for the names of cover types and phases. Indicator species for the cover types and phases are noted in Tables 2–10. Although sim-

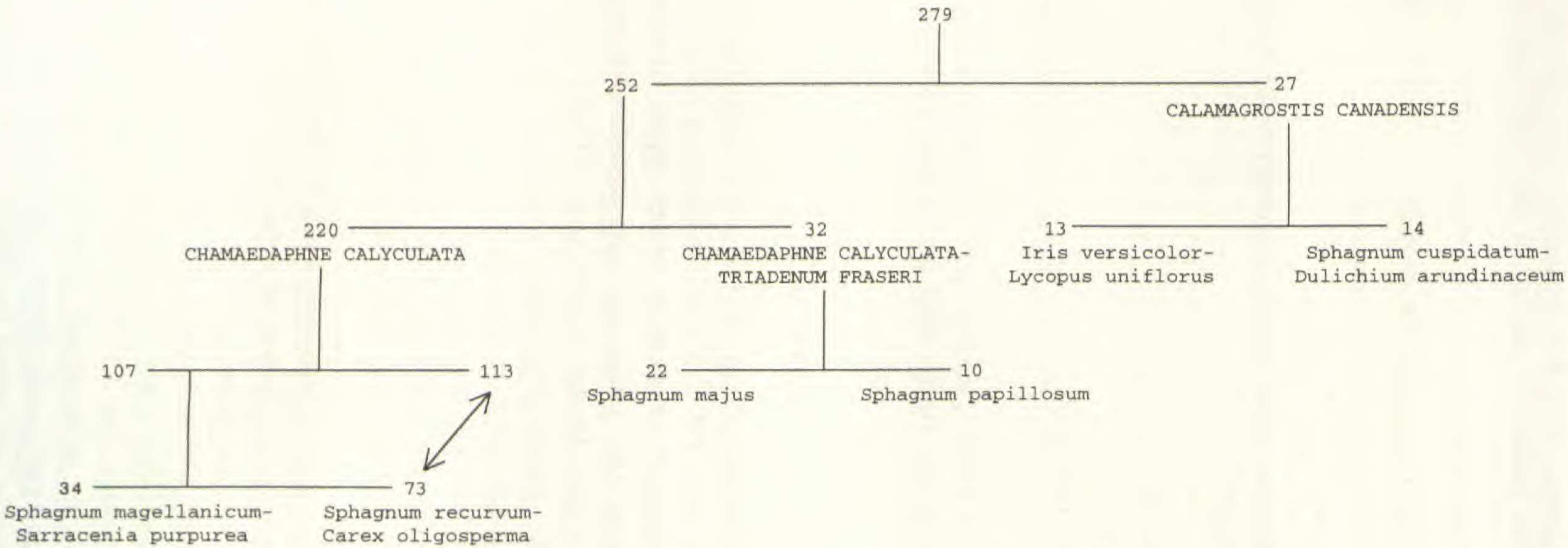

Figure 2. Dendrogram of the vegetation cover types and phases as delineated by TWINSPAN and field observation. Designations in all capital lettering are cover types, designations with capital and lowercase lettering are phases. Numbers refer to the number of quadrats in each cover type or phase. The arrow indicates that the clusters of 113 and 73 plots were combined to form the *Sphagnum recurvum–Carex oligosperma* phase.

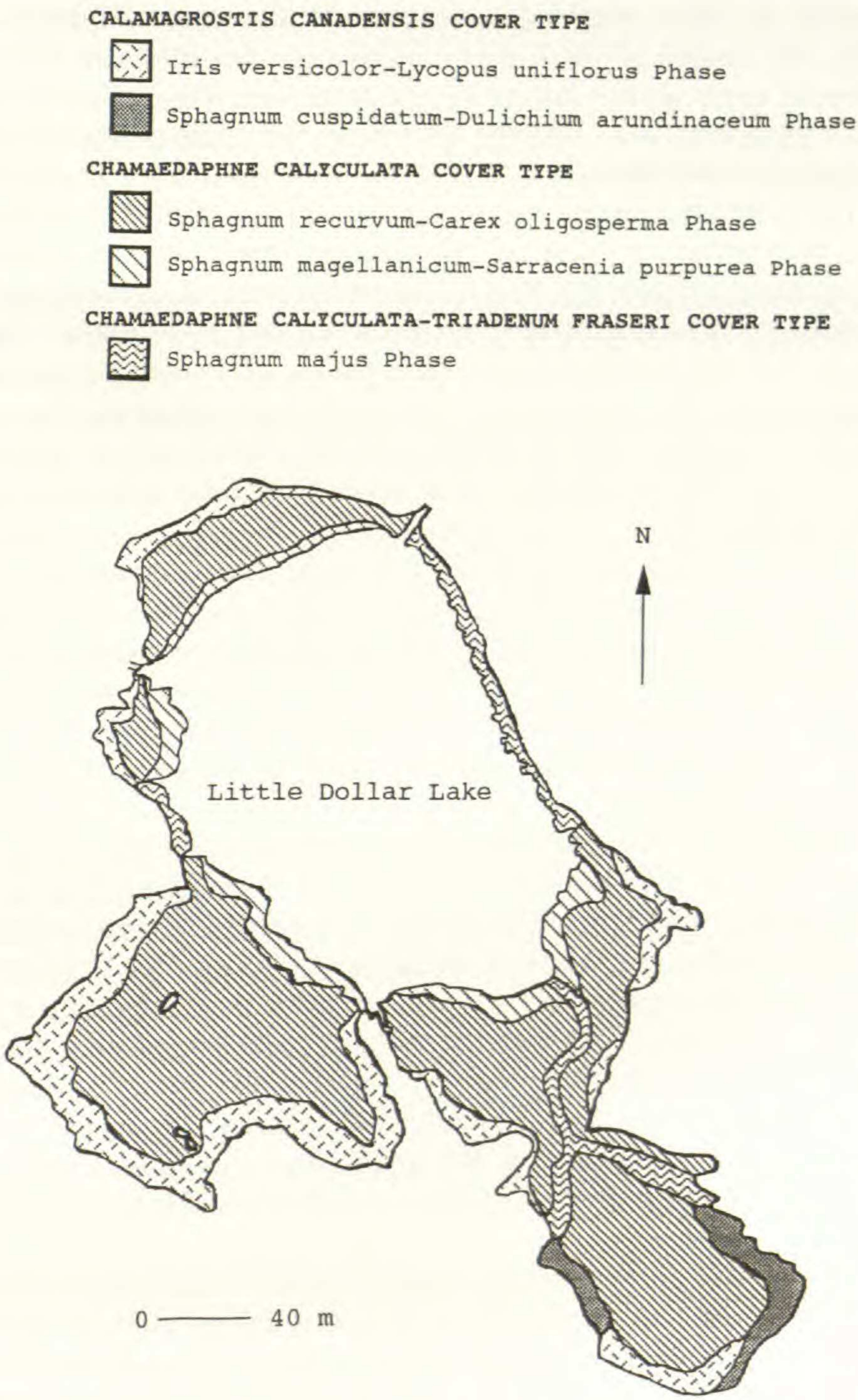

Figure 3. Vegetation map of Little Dollar Lake peatland illustrating the extent of the vegetation cover types and constituent vegetation phases. The *Sphagnum papillosum* phase is not mapped due to its narrow spatial distribution. This phase is present in a narrow (~1.0 m) band along the lake margin in all areas where the *Sphagnum magellanicum–Sarracenia purpurea* phase is present. Scale is approximate.

ilarities to other peatland complexes in the upper Midwest do exist, the names of these communities are not intended to have regional applicability due to the inherent variability of hydrology and topography that directly influences the composition of individual peatland floras.

TWINSPAN classification split the initial set of 279 quadrats into two groups, a group of 252 quadrats and a second group of 27 quadrats (Figure 2). The 27 quadrats were designated as the *Calamagrostis canadensis* CT. At the second level the *C. canadensis* CT was divided further into phases of 13 and 14 quadrats respectively. The cluster of 13 quadrats was named the *Iris versicolor–Lycopus uniflorus* PHS, and the cluster of 14 quadrats was named the *Sphagnum cuspidatum–Dulichium arundinaceum* PHS (Figure 2).

The remaining 252 quadrats were split into two clusters, one cluster of 220 quadrats and one cluster of 32 quadrats. The cluster of 220 quadrats was named the *Chamaedaphne calyculata* CT or "ericaceous scrub," and the cluster of 32 quadrats was named the *C. calyculata–Triadenum fraseri* CT (Figure 2). The two phases of the *C. calyculata* CT consisted of clusters of 186 quadrats and 34 quadrats.

TWINSPAN separated the 220 quadrats of the *Chamaedaphne calyculata* CT into clusters of 107 and 113 quadrats (Figure 2). The cluster of 113 quadrats at the third level had an essentially uniform species composition. In the field, this group of 113 quadrats was indistinguishable from the cluster of 73 quadrats at the fourth cut level. Therefore, the 73 remaining quadrats on the fourth cut level and the entire 113 quadrat dichotomy were combined into a cluster of 186 quadrats (Figure 2). These 186 quadrats were representative of the *Sphagnum recurvum–Carex oligosperma* PHS (hummock-hollow complex) of the *C. calyculata* CT.

The remaining 34 quadrats, isolated from TWINSPAN's cluster of 107 quadrats at the fourth level, had a unique suite of species that corresponded to the floating-mat community along the northern and southern lake margin. This cluster was named the *Sphagnum magellanicum–Sarracenia purpurea* PHS of the *Chamaedaphne calyculata* CT (Figure 2).

Lastly, at the second cut level, the cluster of 32 quadrats that composed the *Chamaedaphne calyculata–Triadenum fraseri* CT was divided into two constituent phases (Figure 2). The *Sphag-*

num majus PHS consisted of 22 quadrats and was associated with the stream channel and the narrow eastern and western mats (Figures 1 and 3). The remaining ten quadrats, the *Sphagnum papillosum* PHS, formed an approximately two to three meter zone immediately bordering the open water of the majority of the peatland.

Species richness and frequency within sampling quadrats. The *Calamagrostis canadensis* CT and the *Chamaedaphne calyculata* CT were the most species rich of the cover types (Table 1). The *C. canadensis* CT was restricted to more minerotrophic lagg areas. Despite being sampled by only 27 quadrats, this cover type contained 54 species. The *C. calyculata* CT was slightly more diverse, but was sampled extensively by 220 quadrats. The most diverse phase was the *Sphagnum recurvum–Carex oligosperma* PHS of the *C. calyculata* CT (Table 1). The next most diverse phase was the *Iris versicolor–Lycopus uniflorus* PHS of the *C. canadensis* CT (Table 1). The *I. versicolor–L. uniflorus* PHS consisted of only 13 quadrats but contained 44 different species. The most species-poor cover type or phase was the *Potamogeton confervoides–Utricularia geminiscapa* CT. With only seven species, this cover type was restricted to the open water of Little Dollar Lake.

The nutrient-poor nature of the peatland was emphasized by the dominance of the Sphagnaceae (peat moss family) and the Ericaceae (heath family) on a visual and a quantitative level within the 279 sampling quadrats. Of the ten most frequent species in the 279 quadrats, eight belonged to either the Sphagnaceae or the Ericaceae (Figure 4). Of these ten species, *Chamaedaphne calyculata* (L.) Moench was the most abundant species, occurring in 258 quadrats (92%). *Vaccinium oxycoccos* L. was second, occurring in 218 quadrats (78%). The most abundant sedge was *Carex oligosperma* Michx. which was present in 106 quadrats (38%).

The tenth most frequent taxon in the 279 quadrats was *Acer rubrum* L. This species was present only as seedlings or small saplings in the quadrats sampled. Seedlings were noted in 23% of the quadrats sampled. In every quadrat in which *A. rubrum* appeared, it had a cover value of less than 2%. Of the ten most abundant species, the only bryophytes were members of the Sphagnaceae (Figure 4).

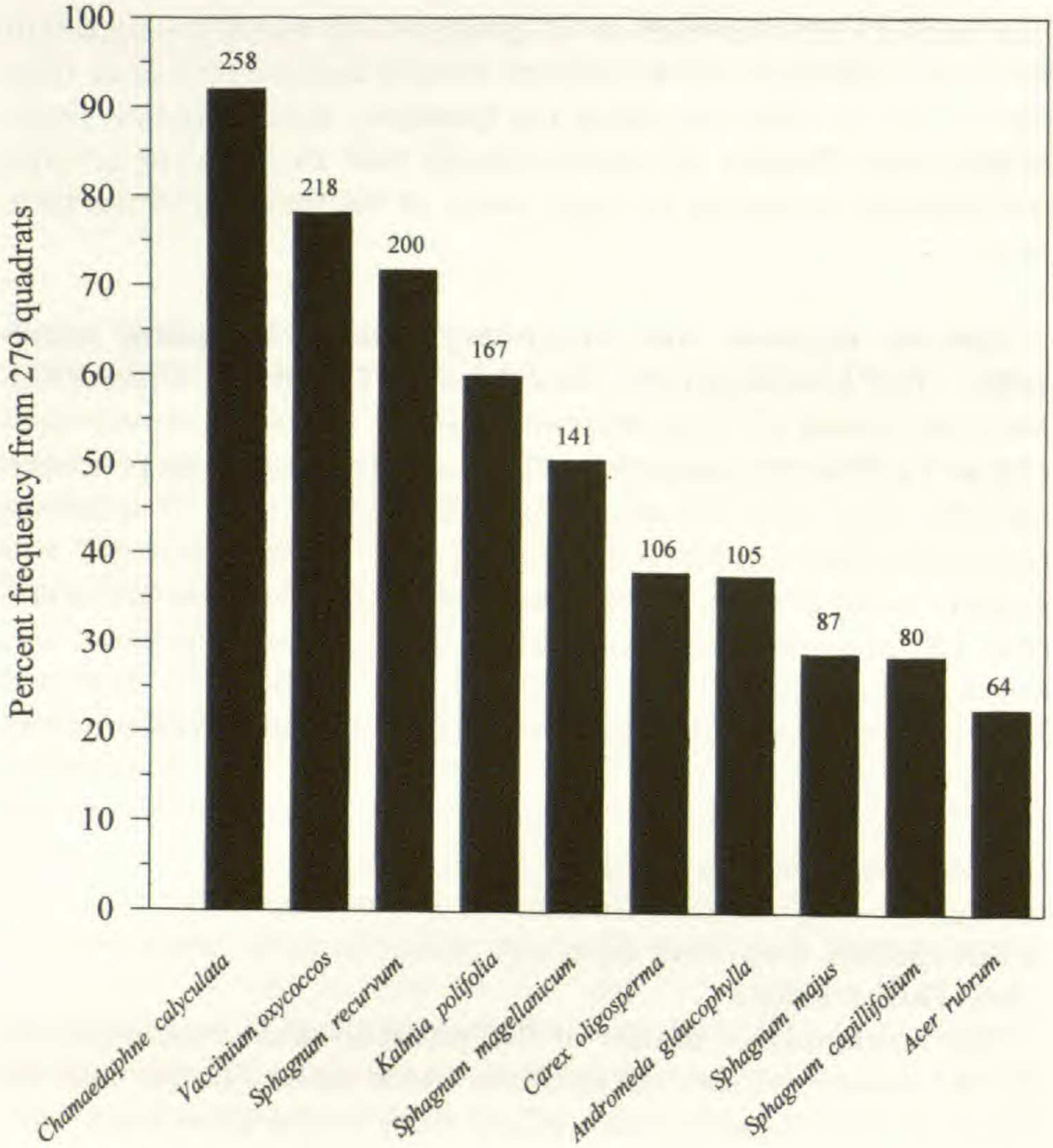

Figure 4. Percent frequency of the ten most abundant species in the 279 quadrats sampled. The number above each bar equals the total number of quadrats in which each species occurred.

DISCUSSION

The vegetation of Little Dollar Lake peatland. The bryophyte flora of Little Dollar Lake peatland consisted of 36 species including eleven species of *Sphagnum.* The vascular flora of the peatland was comprised of 93 species dominated by sedge species (Cyperaceae) and heath species (Ericaceae). The complete bryophyte and vascular flora of Little Dollar Lake peatland, including comments on abundance and habitats, is presented in Hellquist and Crow (1997).

The following discussion summarizes the vegetation patterns at Little Dollar Lake peatland, and emphasizes the presence of various plant species as a means to infer the nutrient status of a peatland or microhabitats within a peatland. The four cover types and the six constituent phases are discussed in a roughly centripetal manner starting with the lagg communities on the outside of the peatland basin and proceeding inward toward Little Dollar Lake.

1. *Calamagrostis canadensis* Cover Type

The outermost portion of a basin peatland is known as the lagg or moat. The lagg is an ecotone (sensu Risser 1995) between the consolidated peat of the open mat and the mineral soils of the upland. The lagg is characterized by shallower, better aerated peat that is enriched by nutrients from the adjacent upland (Crum 1988; Damman and French 1987; Gore 1983). A moat of open water separating the upland from the peatland proper is often found within the lagg area. The lagg is typically one of the most botanically diverse communities within a peatland. The lagg usually contains minerotrophic wetland species that are not exclusively associated with peatland floras except in the context of lagg habitats (Crum 1988). Thus, the species composition of the lagg reflects a more minerotrophic or marsh-like physiognomy compared to the majority of the peatland basin.

The *Calamagrostis canadensis* CT formed an encircling, fen-like community adjacent to the upland on all peatland mats of the basin except the narrow eastern and western mats (Figure 3). In northern Michigan, a *C. canadensis* (Michx.) P. Beauv. association typically follows fire and sometimes develops in the marginal areas of peatlands that are damp, but not extremely wet (Gates 1942). In the summers of 1994 and 1995, this cover type was merely damp with no standing water. In 1996, however, most of this cover type was saturated with water or had standing water 0.25 to 0.50 m in depth, especially in areas of the southwestern mat and southern mat extension.

Sphagnum species were not as prominent in the *Calamagrostis canadensis* CT, with only *S. recurvum* P. Beauv. and *S. cuspidatum* Hoffm. occurring with some frequency (Table 2). *Sphagnum recurvum* was apparent in the open, outer areas of lagg closer to the ericaceous scrub, while *S. cuspidatum* formed lush pockets in the wettest, muckiest areas of the lagg. In 1996, *S. cuspidatum*

Table 2. Mean percent cover and percent frequency of dominant and associated species in the *Calamagrostis canadensis* cover type consisting of 27 quadrats out of 279. Species having less than 10% frequency are not included in the table. *TWINSPAN indicator species. *Lycopus uniflorus* was also designated as an indicator species, but does not appear in the table.

	Mean % Cover	% Frequency
BRYOPHYTES		
Sphagnum recurvum	55	51.9
*Sphagnum cuspidatum**	27	30.0
Warnstorfia fluitans	5	14.8
Calliergon cordifolium	27	11.1
Calliergon stramineum	22	11.1
Callicladium haldanianum	4	11.1
VASCULAR PLANTS		
*Calamagrostis canadensis**	30	88.9
Carex lasiocarpa	38	74.1
Potentilla palustris	5	55.6
Triadenum fraseri	2	44.4
Chamaedaphne calyculata	18	37.0
Acer rubrum	<1	37.0
Lysimachia thyrsiflora	2	30.0
*Iris versicolor**	14	26.0
Glyceria canadensis	26	18.5
Lysimachia terrestris	2	18.5
Galium trifidum	3	15.0
Dulichium arundinaceum	20	14.8
Impatiens capensis	8	14.8
Carex oligosperma	10	11.1
Scutellaria galericulata	5	11.1
Equisetum fluviatile	2	11.1

flourished in the standing water of southern lagg areas with delicate individuals growing to lengths as long as 0.25 m. While there was a lack of *Sphagnum* diversity in this cover type, members of the Amblystegiaceae contributed to the diverse bryophyte flora of this cover type. Members of this minerotrophic-indicative family, *Calliergon cordifolium* (Hedw.) Kindb. and *C. stramineum* (Brid.) Kindb., often were observed thriving in wet, decomposing leaf litter.

The two most frequent and dominant vascular species were *Calamagrostis canadensis* and *Carex lasiocarpa* (Table 2). These two species grew intermingled and gave the lagg community its narrow-leaved graminoid texture that was readily distinguished from the neighboring ericaceous scrub community. At the height of the growing season, the prominence of *C. canadensis* gave the lagg a distinct marsh-like appearance. Other widely scattered, but locally abundant species of this community type included *Galium tinctorium* L., *Iris versicolor* L., *Lysimachia thyrsiflora* L., *L. terrestris* (L.) B.S.P., *Lycopus uniflorus* Michx., and *Potentilla palustris* (L.) Scop.

The species within the graminoid lagg at Little Dollar Lake peatland were similar to the herbaceous component of the lagg at Mud Pond Bog (Moultonborough, NH). Species found in both of these peatlands included *Calamagrostis canadensis, Lycopus uniflorus, Scirpus cyperinus* (L.) Kunth, and *Scutellaria galericulata* L. (C. E. Hellquist, ms. in prep.). The lagg communities at Mud Pond Bog were also characterized by an extensive tall shrub lagg association dominated by *Ilex verticillata* (L.) A. Gray, *Nemopanthus mucronatus* (L.) Trel., *Lyonia ligustrina* (L.) DC., *Vaccinium corymbosum* L., and *Viburnum nudum* L. (C. E. Hellquist, ms. in prep.). At Little Dollar Lake, typical lagg shrubs such as *I. verticillata* and *N. mucronatus* grew infrequently within the peatland basin itself, although both taxa grew abundantly in rich upland soils that immediately fringed the lagg. The presence of *I. verticillata, N. mucronatus,* and *V. nudum* var. *cassinoides* (L.) T. & G. at Little Dollar Lake is reminiscent of the *I. verticillata–N. mucronatus* community type described for northern Michigan kettlehole peatlands (Vitt and Slack 1975). This cover type also resembled the *I. verticillata–Acer–Carex canescens* community type found nearest the upland in Mud Pond Bog (Hillsborough, NH; Dunlop 1987). Species common to these cover types include *I. verticillata, Acer rubrum, Lysimachia terrestris, Lycopus uniflorus,* and *C. canadensis* (Dunlop 1987).

1A. *Iris versicolor–Lycopus uniflorus* Phase

The substrate of the *Iris versicolor–Lycopus uniflorus* PHS (Figure 3) was composed of very shallow peat (<1.0 m) that often was covered by decaying leaf duff from upland trees. The presence of shade-tolerant *Sphagnum squarrosum* Crome emphasized the nutrient-rich nature of the lagg habitat. *Sphagnum squarrosum* typically grows in minerotrophic, alkaline *Thuja occidentalis* L. swamps and swampy woodlands (Andrus 1980; Crum 1983, 1988). The most abundant non-*Sphagnum* bryophyte was *Calliergon cordifolium,* a species that thrived in damp leaf

Table 3. Mean percent cover and percent frequency of dominant and associated species in the *Iris versicolor–Lycopus uniflorus* phase of the *Calamagrostis canadensis* cover type (13 quadrats). Species having less than 10% frequency are not included in the table. *TWINSPAN indicator species.

	Mean % Cover	% Frequency
BRYOPHYTES		
Sphagnum recurvum	60	84.6
Warnstorfia fluitans	3	15.4
*Calliergon cordifolium**	27	23.1
Callicladium haldanianum	4	23.1
Drepanocladus uncinatus	6	15.4
Dicranum flagellare	7	15.4
Pleurozium schreberi	8	15.4
VASCULAR PLANTS		
Calamagrostis canadensis	44	100.0
Carex lasiocarpa	31	69.2
Potentilla palustris	4	61.5
Lycopus uniflorus	7	61.5
Iris versicolor	14	53.8
Acer rubrum	<1	53.8
Triadenum fraseri	3	53.8
Lysimachia terrestris	2	38.5
Impatiens capensis	8	30.8
Galium trifidum	3	30.8
Chamaedaphne calyculata	6	23.1
Scutellaria galericulata	5	23.1
Carex canescens	8	15.4
Carex oligosperma	13	15.4
Viola macloskeyi	6	15.4

litter with *Warnstorfia fluitans* (Hedw.) Loeske [*Drepanocladus fluitans* (Hedw.) Warnst.]. Several bryophyte taxa were restricted to this phase including the leafy liverworts *Chiloscyphus polyanthos* (L.) Corda and *Lophocolea heterophylla* (Schrad.) Dum., as well as the mosses *Climacium dendroides* (Hedw.) Web. & Mohr. and *Plagiothecium denticulatum* (Hedw.) Schimp. in B.S.G.

Dominant vascular species included the same suite of species that defined the graminoid lagg cover type as a whole (*Calamagrostis canadensis, Carex lasiocarpa,* and *Iris versicolor*; Table 3). The prominence of *I. versicolor* and *Lysimachia terrestris* made this phase readily apparent in the field. Northern Michigan peatlands may have a fringing *Iris* association less than a meter wide (Gates 1942). At Little Dollar Lake, *I. versicolor* was a prominent component of the *C. canadensis* CT with a distribution several meters in width, especially in the lagg areas of the southern-oriented peatland mats.

Within the *Iris versicolor–Lycopus uniflorus* PHS there was one locality that had an entirely unique species composition compared to the rest of the peatland. This area was situated within the lagg of the southwestern mat (Figure 1) in an area that apparently was influenced by runoff from a seasonal, dirt truck trail (Hellquist 1996). In this area, *Typha latifolia* L. was well established. Futyma (1982) noted the presence of *Typha* in the basin in the early 1980s, but made no reference to the location of the colony. Other species essentially limited to this distinct lagg habitat were *Carex stipata* Muhl., *Epilobium ciliatum* Raf., *Polygonum cilinode* Michx., *Rubus canadensis* L., *Scutellaria lateriflora* L., and *Rumex obtusifolius* L.

1B. *Sphagnum cuspidatum–Dulichium arundinaceum* Phase

The *Sphagnum cuspidatum–Dulichium arundinaceum* PHS occurred in two distinct areas in the southeastern and western lagg areas of the southern mat extension (Figure 3). This association was apparent in the wettest areas of lagg that contained exposed, mucky peat. In 1996, this area was covered by standing water roughly 0.25 to 0.50 m deep. The most frequent vascular species of this phase included *Calamagrostis canadensis, Carex lasiocarpa, Chamaedaphne calyculata,* and *Potentilla palustris.* Thirteen species with greater than 10% frequency were present including *Glyceria canadensis* (Michx.) Trin., *Carex utriculata* F. Boott, *Equisetum fluviatile* L., and *Salix pedicellaris* Pursh (Table 4).

The dominant peat mosses of this phase were *Sphagnum recurvum* and *S. cuspidatum* (Table 4). Other important bryophyte species included members of the Amblystegiaceae such as *Warnstorfia fluitans, W. exannulata* (Schimp. in B.S.G.) Loeske [*Drepanocladus exannulatus* (Schimp. in B.S.G.) Warnst.], *Calliergon cordifolium,* and *C. stramineum.* Despite its infrequency in the quantitative sampling of this phase, *W. exannulata* formed an almost homogeneous bryophyte cover on exposed, mucky peat in the southeastern lagg of the southern mat extension. In 1996, this same population of *W. exannulata* was still vigorous despite being submerged in standing water. *Warnstorfia exannulata* is considered a dominant species of poor fens in Alberta along with *Sphagnum angustifolium* (C. Jens. ex Russ.) C. Jens., *S. majus*

Table 4. Mean percent cover and percent frequency of dominant and associated species in the *Sphagnum cuspidatum–Dulichium arundinaceum* phase of the *Calamagrostis canadensis* cover type (14 quadrats). Species having less than 10% frequency are not included in the table. *TWINSPAN indicator species.

	Mean % Cover	% Frequency
BRYOPHYTES		
Sphagnum recurvum	38	21.4
*Sphagnum cuspidatum**	27	57.1
Warnstorfia fluitans	8	14.3
Sphagnum majus	<1	14.3
Calliergon stramineum	30	14.3
Calliergon cordifolium	27	11.1
VASCULAR PLANTS		
*Calamagrostis canadensis**	14	78.6
*Carex lasiocarpa**	43	78.6
Chamaedaphne calyculata	24	50.0
Potentilla palustris	5	50.0
*Lysimachia thyrsiflora**	1	35.7
Triadenum fraseri	<1	35.7
Glyceria canadensis	32	28.6
*Dulichium arundinaceum**	20	28.6
Acer rubrum	<1	21.4
Carex utriculata	8	14.3
Vaccinium macrocarpon	3	14.3
Equisetum fluviatile	2	14.3
Salix pedicellaris	23	14.3

(Russ.) C. Jens., and *S. jensenii* H. Lindb. (Vitt and Chee 1990). Although members of the Amblystegiaceae tend to prefer more minerotrophic microhabitats, *W. fluitans* and *C. stramineum* seem to occur in acid to intermediate acid habitats (ca. pH 3.7–6.0; Gorham and Janssens 1992b).

At Little Dollar Lake, several emergent vascular species colonized this rich muck including *Carex lasiocarpa, Dulichium arundinaceum* (L.) Britton, *Glyceria borealis* (Nash) Batchelder, *Juncus alpinus* Vill., *Potentilla palustris,* and *Puccinellia pallida* (Torr.) R. T. Clausen. The only locality of *Carex chordorrhiza* L. f. was in the exposed peat of the southeastern lagg. *Carex chordorrhiza* is considered a species indicative of poor fens in Minnesota (Wheeler et al. 1983) and rich fen conditions in Alberta (Vitt and Chee 1990).

Table 5. Mean percent cover and percent frequency of dominant and associated species in the *Chamaedaphne calyculata* cover type (220 quadrats). Species having less than 10% frequency are not included in the table. *TWINSPAN indicator species.

	Mean % Cover	% Frequency
BRYOPHYTES		
Sphagnum recurvum	74	83.2
Sphagnum majus	50	36.3
*Sphagnum magellanicum**	14	26.5
Aulocomnium palustre	6	13.3
*Sphagnum capillifolium**	18	10.6
VASCULAR SPECIES		
Chamaedaphne calyculata	46	99.1
Carex oligosperma	26	94.7
Kalmia polifolia	15	62.8
Andromeda glaucophylla	11	36.3
Acer rubrum	<1	27.4
*Vaccinium oxycoccos**	7	14.2

2. *Chamaedaphne calyculata* Cover Type

The *Chamaedaphne calyculata* CT was unquestionably the most prominent cover type within the peatland (Figure 3). Members of the Ericaceae lent this cover type its scrubby, homogeneous appearance. These shrubs occurred more or less continuously across a mosaic of hummocks and hollows carpeted by several species of *Sphagnum.* The *Sphagnum recurvum–Carex oligosperma* PHS was characterized by the grounded hummock-hollow complex. The *Sphagnum magellanicum–Sarracenia purpurea* PHS formed narrow bands of quaking mat that fringed the majority of the lake (Figure 3).

The three dominant ericaceous shrubs of this cover type were *Chamaedaphne calyculata, Kalmia polifolia* Wangenh., and *Andromeda glaucophylla* Link (Table 5). The prostrate ericad *Vaccinium oxycoccos* was also apparent in this community, with individuals winding over *Sphagnum* and between branches of ericaceous shrubs on relatively open hummocks. *Carex oligosperma,* the most ubiquitous sedge of the peatland, was also characteristic of this cover type.

In northern Michigan, the *Chamaedaphne calyculata* association is the most ubiquitous in the region and is found extensively in almost every peatland (Gates 1942). *Andromeda glaucophylla,* *Kalmia polifolia, Ledum groenlandicum* Oeder, and *Vaccinium oxycoccos* are considered secondary components of the association (Gates 1942). All of the heath species at Little Dollar Lake, with the exception of *L. groenlandicum,* were readily apparent in the *C. calyculata* CT. At Little Dollar Lake, *L. groenlandicum* was scattered widely across the ericaceous scrub and was restricted to large, dry hummocks.

Schwintzer (1981) noted that "bogs" (i.e. poor fens) in northern Michigan were often dominated by ericaceous shrubs and *Sphagnum* spp. and suggested that their dominance in these habitats was due to reduced rheotrophic conditions in these peatlands. Vitt and Slack (1975) found that *Chamaedaphne calyculata* had wide habitat preferences and therefore was not directly linked to any discrete association of *Sphagnum* species. In the Northeast, the *C. calyculata* association is affiliated with oligotrophic to ombrotrophic sites under very wet conditions (Damman and French 1987). The dominance of *C. calyculata* in large expanses of peatland has been noted by many investigators (e.g. Crow 1969; Dunlop 1987; Fahey 1993; Fahey and Crow 1995; Schwintzer 1981; Vitt and Bayley 1984; Vitt and Slack 1975).

The *Chamaedaphne calyculata* CT at Little Dollar Lake resembled the "closed mat zone" of Vitt and Slack (1975) that was present in all eight of their northern Michigan study sites. This zone was distinguished by the presence of a tree layer of varying extent as well as an extensively developed ericaceous shrub layer (Vitt and Slack 1975). There was no tree canopy or evergreen parkland at Little Dollar Lake, despite the presence of several coniferous tree species including *Picea mariana* (Miller) B.S.P., *Abies balsamea* (L.) Miller, *Pinus strobus* L., and *Larix laricina* (Duroi) K. Koch that were widely dispersed on the peatland mat. *Picea mariana* and *L. laricina* become abundant in peatlands with low water tables and well-drained peats (Glaser 1987). The reduced prominence of these species at Little Dollar Lake may be indicative of a high water table.

The most abundant conifer in this cover type was *Pinus strobus,* represented by both saplings and several mature trees growing on the mat. Although *P. strobus* is not regarded as a wetland tree, this species is often found within peatlands (e.g. Crow 1969; Dunlop 1987; Fahey and Crow 1995; Miller 1996; Schwintzer 1981; C. E. Hellquist, ms. in prep.). In peatlands, *P. strobus* often grows to mature heights of several meters, but these individuals typically are unhealthy and chlorotic (Miller 1996; C. E. Hellquist, pers. obs.).

2A. *Sphagnum recurvum–Carex oligosperma* Phase

This phase occupied expanses of grounded mat that exhibited the undulating topography characterized by *Sphagnum* hummocks that rise up to a meter above shallow, trough-like hollows (Figure 3). The species composition of the hummock-hollow complex is maintained in part by the growth and autogenic successional trends of *Sphagnum* species. *Sphagnum* grows apically over individuals so that their stems build up a microtopography of undulating mounds (hummocks) that are supported by a scaffolding formed by the roots and branches of vascular plant species, especially ericaceous shrubs (van Breeman 1995; Vitt et al. 1975).

A highly overlapping, directional succession of *Sphagnum* taxa occurs along the hummock-hollow gradient (Andrus 1986; Andrus et al. 1983; Crum 1988; Horton et al. 1979; Vitt and Slack 1984; Vitt et al. 1975). *Sphagnum* species characteristic of hummocks have high water-storing capacity, greater capillary pull, higher productivity under nutrient-deficient conditions, a greater cation exchange capacity due to the higher quantities of polyurionic acids produced during growth, and an ability to inhabit self-maintained low pH microhabitats (Clymo and Hayward 1982; Moore and Bellamy 1974; Rydin 1985; Spearing 1972; van Breeman 1995; Vitt et al. 1975).

Due to the nutrient-poor nature of this cover type, the vegetation was dominated by *Sphagnum* species including *S. majus, S. recurvum, S. magellanicum* Brid., and *S. capillifolium* (Ehrh.) Hedw. Ericaceous species including *Chamaedaphne calyculata, Kalmia polifolia, Andromeda glaucophylla,* and *Vaccinium oxycoccos,* as well as *Carex oligosperma* were the other ubiquitous species of this cover type (Table 6). The four *Sphagnum* species are most abundant at the acid end of the pH spectrum from approximately pH 3.7 to 5.0 (Gorham and Janssens 1992b). The prominence of *C. calyculata, C. oligosperma,* and *Sphagnum* spp. in open oligotrophic mats is a frequent association in northern Michigan (Schwintzer 1981).

Hollows are depressed areas where the water table typically pools at or just below the surface, often forming a waterlogged trough. These niches tend to have more plentiful nutrient supplies and higher pH values than hummocks (Crow 1969; Crum 1988;

Table 6. Mean percent cover and percent frequency of dominant and associated species in the *Sphagnum recurvum–Carex oligosperma* phase of the *Chamaedaphne calyculata* cover type (186 quadrats). Species having less than 10% frequency are not included in the table. *TWINSPAN indicator species. *Sphagnum fuscum* and *Drosera rotundifolia* also were designated as indicator species for the 73 quadrat cluster of this cover type but do not appear in the table.

	Mean % Cover	% Frequency
BRYOPHYTES		
*Sphagnum recurvum**	58	85.5
Sphagnum magellanicum	34	53.8
Sphagnum capillifolium	22	29.0
*Sphagnum majus**	47	25.8
Aulocomnium palustre	4	16.7
VASCULAR SPECIES		
Chamaedaphne calyculata	42	98.8
Carex oligosperma	22	93.5
Kalmia polifolia	17	71.5
*Andromeda glaucophylla**	15	43.0
*Vaccinium oxycoccos**	25	39.2
Acer rubrum	<1	25.3

Moore and Bellamy 1974; Vitt and Slack 1975; Vitt et al. 1975). *Sphagnum* species that inhabit hollows have a loose, flimsy appearance. These taxa are characterized by sparser and more elongate pendant branches, less efficient water retention and capillary pull, and a reduced production of polyuronic acids (Crum 1988; Moore and Bellamy 1974; Rice and Scheupp 1995; Rydin 1985; Spearing 1972; van Breeman 1995). These features may have been evolutionarily derived as a means to minimize resistance to gas exchange, therefore increasing the carbon assimilating capabilities of the aquatic *Sphagnum* species (Rice and Scheupp 1995).

The hummock-hollow bryophyte zonation at Little Dollar Lake followed a more or less typical sequence described for oligotrophic peatlands in northern Michigan (Crum 1988; Vitt et al. 1975) and Minnesota (Wheeler et al. 1983). From a hollow to the top of a hummock, the general sequence of *Sphagnum* species at Little Dollar Lake was *S. majus, S. recurvum, S. magellanicum, S. papillosum* Lindb., *S. capillifolium,* and *S. fuscum* (Schimp.) Klingrr.

Sphagnum majus inhabited the lowest, dampest troughs of the scrub, and is a species that may grow submerged or emergent. It is characteristic of hollows in open sedge mats and low areas in open laggs (Crum 1983). Frequently found with *S. majus* in saturated hollows was the moss *Warnstorfia fluitans,* and two liverworts, the relatively abundant *Cladopodiella fluitans* (Nees) Joerg., and the more scarce and minute *Cephaloziella elachista* (Jack) Schiffn. *Cladopodiella fluitans* is typically found in sunken microhabitats (e.g. deer trails) where water may accumulate (Crum 1988). At Little Dollar Lake, both of these leafy liverwort species grew in similar microhabitats and were primarily found interwoven among moist *Sphagnum* stems.

Sphagnum recurvum was abundant along the upper edges of the hollows. Colonies of *S. recurvum* usually blended into *S. magellanicum* and *S. capillifolium* along the sides of hummocks. *Sphagnum recurvum* is known to form "loose" carpets in the Great Lakes region (Crum 1983, 1988; Vitt et al. 1975). *Sphagnum recurvum* is abundant in mesotrophic microhabitats such as hollows in open peatland mats (Crum 1983), and thrives under acidic conditions with low calcium and magnesium concentrations (Vitt and Slack 1975). *Sphagnum recurvum* also has been noted as the dominant peat moss in some Ohio peatlands (Andreas and Bryan 1990). In New York, *S. recurvum* is considered to be indicative of "weakly minerotrophic" conditions and is found in poor fen habitats (Andrus 1980).

Growing among *Sphagnum majus* and *S. recurvum* was *Carex oligosperma,* the most abundant sedge in the peatland. *Carex oligosperma* inhabited open hollows throughout the grounded mat and is abundant in acidic northern Michigan basin peatlands (Vitt and Slack 1975). The presence of *Chamaedaphne calyculata* and *C. oligosperma* has been associated with oligotrophic nutrient regimes (Vitt and Bayley 1984). In the Red Lake peatland of Minnesota, heliophilous *C. oligosperma* is a dominant species of open ombrotrophic and poor fen habitats within boreal patterned peatlands (Glaser 1987; Wheeler et al. 1983). Common species that occur with *C. oligosperma* at Red Lake peatland are identical to species found at Little Dollar Lake including *Andromeda glaucophylla, C. calyculata, Eriophorum vaginatum* L. [*E. spissum* Fern.], *Kalmia polifolia, Ledum groenlandicum,* and *Vaccinium oxycoccos* (Wheeler et al. 1983). In Maine, similar communities dominated by *S. recurvum, S. magellanicum, C. oligosperma,* and

C. calyculata have been delineated over wide ranges of minerotrophic conditions (Anderson and Davis 1997).

At Little Dollar Lake, as elevation along the microtopographical gradient increased, *Sphagnum recurvum* abundance dwindled and *S. magellanicum* became prominent. This same pattern has been observed in other northern Michigan peatlands (Vitt and Slack 1975; Vitt et al. 1975). In some areas of Little Dollar Lake peatland, *S. papillosum* had a patchy distribution among *S. magellanicum* on low hummocks or on the sides of taller hummocks. *Warnstorfia fluitans,* a widespread northern moss species often found in acidic to moderately acidic conditions (Crum 1983; Janssens and Glaser 1986), also tended to inhabit moist nooks on the sides or bases of hummocks.

Near the tops of hummocks *Sphagnum magellanicum* faded out of prominence and blended into compact colonies of *S. capillifolium. Sphagnum magellanicum* and *S. capillifolium* are typical of poor fen (oligotrophic) mat habitats (Andrus 1980; Crum 1983, 1988). *Sphagnum magellanicum* and *S. capillifolium* are known to initiate hummocks and grow on the sides or tops of low hummocks (Crum 1983, 1988; Vitt and Slack 1975). *Sphagnum magellanicum* has an especially wide ecological amplitude across the hummock-hollow complex (Vitt and Slack 1975; Vitt et al. 1975).

Hummock tops are generally considered the driest, most nutrient depleted, and most acidic microhabitats along the hummock-hollow sequence (Andrus 1986; Crum 1988; Vitt et al. 1975). The tallest hummocks at Little Dollar Lake often were crowned with compact populations of *Sphagnum fuscum. Sphagnum fuscum* is frequently found on hummock tops (Vitt et al. 1975). *Sphagnum fuscum* is typical of open acid peatland habitats and is strongly indicative of oligotrophic conditions (Crum 1983) as well as "ombrotrophic to weakly minerotrophic" conditions (Andrus 1986). Often intermingled with *S. fuscum* on larger hummocks were *Polytrichum strictum* Brid. [*P. juniperinum* Hedw. var. *affine* (Funck) Brid.], *Calliergon stramineum, Dicranum undulatum* Brid., *Aulocomnium palustre* (Hedw.) Schwaegr., and *Bryum capillare* Hedw. *Polytrichum strictum* is associated with dry, oligotrophic hummock tops (Andrus et al. 1983; Crum 1983; Janssens and Glaser 1986; Vitt 1990; Vitt et al. 1975). *Calliergon stramineum* prefers damp microhabitats in bogs and fens (Crum 1983) and can inhabit acidic to moderately acidic conditions

(Gorham and Janssens 1992b). *Dicranum undulatum* is typically found in open peatland habitats especially on hummocks (Crum 1983).

An additional factor influencing the vegetation dynamics in this cover type was the presence of the caterpillars of the Chain-Spotted Geometer (*Cingilia catenaria* Drury, Lepidoptera: Geometridae), a pale white-colored moth whose caterpillars fed voraciously on ericaceous shrubs on the southwestern and southern mats of Little Dollar Lake peatland. This caterpillar is known to be an occasional pest on blueberry crops and has infested Ontario peatlands, often with severe consequences (McGuffin 1987; Reader 1979). Despite the wide-ranging feeding preferences reported for the Chain-Spotted Geometer (Franklin 1948; McGuffin 1987), at Little Dollar Lake it was observed specifically defoliating *Chamaedaphne calyculata, Kalmia polifolia,* and *Andromeda glaucophylla* (see Hellquist 1996 for further details of the Little Dollar Lake infestations).

2B. *Sphagnum magellanicum–Sarracenia purpurea* Phase

The *Sphagnum magellanicum–Sarracenia purpurea* PHS formed the relatively stable floating mat that was present within five to twenty meters of the lake margin on all mats except the eastern and western mats (Figure 3). This quaking mat was situated between the lake margin and the grounded mat and was easily distinguished by level expanses of peat mosses ("*Sphagnum* lawns"). The *Sphagnum* lawns at Little Dollar Lake were best developed along the lake margin on the northwestern, southwestern, and southern mats (Figure 3). These lawns had a gently undulating topography that was formed primarily by carpets of *S. magellanicum, S. capillifolium,* and *S. papillosum.* The lawn itself had the consistency of a saturated sponge, and was covered by sprigs of ericaceous shrubs, especially *Chamaedaphne calyculata* and *Kalmia polifolia* (Table 7). The height differential of the low sprig-like ericads of the *Sphagnum* lawn and waist-high shrubby ericads on the grounded mat was conspicuous.

Sarracenia purpurea L., *Scheuchzeria palustris* L., and *Eriophorum virginicum* L. thrived on the *Sphagnum* lawn where these species obtained their greatest prominence. In Ontario, where *Chamaedaphne calyculata* was less prominent, oligotrophic indicator species such as *Scheuchzeria palustris, Eriophorum* spp. and bryophytes including *Cladopodiella fluitans, Sphagnum ma-*

Table 7. Mean percent cover and percent frequency of dominant and associated species in the *Sphagnum magellanicum–Sarracenia purpurea* phase of the *Chamaedaphne calyculata* cover type (34 quadrats). Species having less than 10% frequency are not included in the table. *TWINSPAN indicator species.

	Mean % Cover	% Frequency
BRYOPHYTES		
Sphagnum magellanicum	31	100.0
Sphagnum capillifolium	30	64.7
*Sphagnum majus**	28	58.8
Sphagnum papillosum	30	55.9
Sphagnum recurvum	20	38.2
Cladopodiella fluitans	4	23.5
Sphagnum cuspidatum	18	5.9
VASCULAR PLANTS		
Chamaedaphne calyculata	23	100.0
Kalmia polifolia	14	91.2
Vaccinium oxycoccos	23	88.2
Carex oligosperma	20	88.2
Andromeda glaucophylla	8	67.6
*Sarracenia purpurea**	10	52.9
Drosera rotundifolia	1	52.9
Eriophorum virginicum	2	26.5
Rhynchospora alba	3	14.7

jus, S. recurvum, and *Warnstorfia fluitans,* had an increased prevalence (Vitt and Bayley 1984). At Little Dollar Lake, this same suite of species was observed on the *Sphagnum* lawns.

The *Sphagnum* lawn was also the only habitat in the peatland where the orchids *Calopogon tuberosus* (L.) B.S.P. and *Pogonia ophioglossoides* (L.) Ker Gawler grew. *Calopogon tuberosus* grew in all *Sphagnum* lawn habitats, whereas *P. ophioglossoides* was limited to the lawn of the northwestern mat. Both of these orchids are abundant in northern Michigan peatlands, but were surprisingly scarce at Little Dollar Lake.

The *Sphagnum magellanicum–Sarracenia purpurea* PHS on the northwestern floating mat was pock-marked by large, irregular holes in the mat that often were colonized by two submersed species, *Potamogeton confervoides* Reichb. and *Utricularia geminiscapa* Benj. Presumably, these holes had been accentuated and possibly maintained by beaver activity. The edges of these holes were fringed with exposed peat and were the only sites for *Ly-*

copodiella inundata (L.) Holub [*Lycopodium inundatum* L.] and *Drosera intermedia* Hayne. Other species that grew on this exposed peat included *D. rotundifolia* L., *Eriocaulon aquaticum* (Hill) Druce [*E. septangulare* With.], *Menyanthes trifoliata* L., *Rhynchospora alba* (L.) Vahl., and the liverwort *Cladopodiella fluitans*.

The *Sphagnum magellanicum–Sarracenia purpurea* PHS closely resembled a similar community at Mud Pond Bog (Moultonborough, NH). Both lawn communities were saturated, spongy habitats extensively colonized by insectivorous plants (*Sarracenia purpurea, Drosera intermedia,* and *D. rotundifolia*), as well as stunted ericaceous species, especially *Chamaedaphne calyculata* (C. E. Hellquist, ms. in prep.). These lawn habitats at Moultonborough were also the preferred habitats of *Pogonia ophioglossoides* and *Calopogon tuberosus* (C. E. Hellquist, ms. in prep.) and corresponded well to the *Sphagnum* lawn concept of Crum (1988). The *Vaccinium oxycoccos–Rhynchospora alba* subtype of Mud Pond Bog (Hillsborough, NH), characterized by dwarfed ericaceous shrubs as well as *D. rotundifolia* and *S. purpurea* (Dunlop 1987), also was similar to the species assemblage at Little Dollar Lake. In Ohio, similar species inventories have been recorded in *Sphagnum* lawn communities (Andreas and Bryan 1990).

3. *Chamaedaphne calyculata–Triadenum fraseri* Cover Type

The *Chamaedaphne calyculata–Triadenum fraseri* CT was composed of two phases that exhibited possible terrestrialization patterns in two distinct areas of the peatland. One phase of this cover type was associated with terrestrialization at the lake margin (the *Sphagnum papillosum* PHS) and the other phase was associated with terrestrialization of the stream channel (the *S. majus* PHS; Figure 3). This cover type has been renamed and is identical to the *C. calyculata–Carex lasiocarpa* CT first described by Hellquist (1996) at Little Dollar Lake.

This cover type represents a hybrid association colonized by species common to both the *Chamaedaphne calyculata* CT and the *Calamagrostis canadensis* CT (Table 8). Few species were restricted to this cover type, thus it is defined more by the absence of certain species than those present in its marsh-like physiognomy. Despite its low cover value, *Triadenum fraseri* (Spach) Gleason was a frequent component of this cover type and was

Table 8. Mean percent cover and percent frequency of dominant and associated species in the *Chamaedaphne calyculata–Triadenum fraseri* cover type (32 quadrats). Species having less than 10% frequency are not included in the table. *TWINSPAN indicator species. *Sphagnum cuspidatum* also was designated as an indicator species, but does not appear in the table.

	Mean % Cover	% Frequency
BRYOPHYTES		
*Sphagnum recurvum**	45	50.0
*Sphagnum majus**	60	34.4
*Sphagnum papillosum**	44	28.1
Sphagnum magellanicum	13	18.8
VASCULAR PLANTS		
Chamaedaphne calyculata	44	93.8
Triadenum fraseri	3	59.4
Carex lasiocarpa	31	56.3
*Carex oligosperma**	15	34.4
Vaccinium macrocarpon	26	34.4
*Carex canescens**	25	25.0
Calamagrostis canadensis	24	21.9
Drosera rotundifolia	1	21.9
Carex utriculata	4	18.8
Glyceria canadensis	2	18.8
Acer rubrum	<1	18.8
Potentilla palustris	3	12.5
*Sarracenia purpurea**	4	12.5

readily apparent with its distinct growth form and reddish-hued foliage (Table 8). *Triadenum fraseri* was commonly seen in more minerotrophic microhabitats along the lakeshore, stream channel, and in the lagg.

Although prominent in the *Calamagrostis canadensis* CT, *Carex lasiocarpa* was also conspicuous in this cover type with a cover of 31% and 56.3% frequency. In the stream channel, the distinct physiognomy of the *C. lasiocarpa* community traced the course of the stream channel from its origin in the muck pools of the southern mat extension, through the ericaceous scrub of the southern mat to the open water of the lake (Figures 1 and 3).

Carex lasiocarpa is indicative of more minerotrophic conditions (e.g., Crum 1988; Jeglum 1971; Schwintzer 1978; Vitt and Bayley 1984; Vitt and Slack 1975). With its prolific interlaced rhizome sytems, *C. lasiocarpa* is one of the most important lake-fill species that can initiate the process of terrestrialization along shorelines (Gates 1942). In northern Michigan, *C. lasiocarpa* is

Table 9. Mean percent cover and percent frequency of dominant and associated species in the *Sphagnum majus* phase of the *Chamaedaphne calyculata–Triadenum fraseri* cover type (22 quadrats). Species having less than 10% frequency are not included in the table. *TWINSPAN indicator species.

	Mean % Cover	% Frequency
BRYOPHYTES		
*Sphagnum recurvum**	51	63.6
*Sphagnum majus**	64	45.5
VASCULAR PLANTS		
Chamaedaphne calyculata	43	95.5
*Carex oligosperma**	15	45.5
*Calamagrostis canadensis**	28	27.3
*Vaccinium macrocarpon**	40	27.3
Carex utriculata	5	22.7
Glyceria canadensis	3	22.7
Acer rubrum	<1	22.7
Potentilla palustris	3	18.2
Drosera rotundifolia	<1	18.2
Carex canescens	8	13.6

the primary mat-forming species along more alkaline lake margins with circumneutral pH values (Crum 1988; Vitt and Slack 1975). A circumneutral sedge mat dominated by *C. lasiocarpa* has also been noted in southern Michigan (Crow 1969). At Red Lake peatland in Minnesota, *C. lasiocarpa* was the most abundant vascular plant in open rich fens (Wheeler et al. 1983). Similarly, in north-central New Hampshire, the presence of *C. lasiocarpa* along lake edges and in wet habitats with a fen-like flora has also been noted (Fahey and Crow 1995; C. E. Hellquist, ms. in prep.).

3A. *Sphagnum majus* Phase

The *Sphagnum majus* PHS was a relatively minerotrophic phase that was contained within the stream channel that originated in the southeastern lagg of the southern mat extension, and eventually reached the open water of Little Dollar Lake. The *S. majus* PHS also comprised the narrow eastern and western mats (Figure 3). Both of these mats bordered steep upland slopes and were dominated by *S. majus* and *S. recurvum* (Table 9). Conspicuous vascular plants on these mats included *Carex canescens, C. lasiocarpa, Calla palustris* L., *Chamaedaphne calyculata, Vaccinium macrocarpon* Aiton, and *Triadenum fraseri*. The relative minerotrophy of this vegetation phase was strongly suggested by the presence of *S. subsecundum.* This minerotrophic species is often found in open, wet lagg habitats and sedge mats (Andrus 1980; Crum 1983, 1988), and has been shown to grow in moderately acidic habitats (ca. pH 4.5–6.0; Gorham and Janssens 1992b). This phase was the only area in the peatland where *S. subsecundum* grew in abundance (Hellquist and Crow 1997).

3B. *Sphagnum papillosum* Phase

The *Sphagnum papillosum* PHS occurred along the majority of the lake margin. This community was distinguished by a narrow swath (~1.0 m) of *Chamaedaphne calyculata* and *Kalmia polifolia* intermingled with *Vaccinium macrocarpon* and *Triadenum fraseri* that extended into the open water of the lake. Immediately behind this band of *C. calyculata* was a wet trough with some standing water, colonized primarily by *S. papillosum, Carex canescens* L., *C. limosa* L., and *Rhynchospora alba.* Although sampled infrequently, *C. limosa* was a major component of this phase. Other species frequent in this trough included *Cladopodiella fluitans, Sphagnum cuspidatum, S. recurvum, Carex lasiocarpa,* and *Sarracenia purpurea* (Table 10).

The *Sphagnum papillosum* PHS of Little Dollar Lake closely resembled an "acid lake edge" community (Crum 1988; Vitt and Slack 1975) that was also observed at Heath Pond Bog, New Hampshire (Fahey 1993). The acid lake vegetation sequence is characterized by the lack of vascular macrophytes in the lake itself, the presence of *Chamaedaphne calyculata* growing out into open water, *Sphagnum* as a pioneer among *C. calyculata,* frequently a "sparse *Carex* fringe" along the lake, and a narrow *Sphagnum* lawn that quickly merges into a grounded mat (Crum 1988).

Vitt and Slack (1975) defined the "acid lake edge" community by the presence of a *Sphagnum cuspidatum–Sphagnum papillosum–Carex limosa–Carex paupercula* association and a pH range of 5.0–7.0. At Little Dollar Lake, *S. papillosum,* and to a lesser extent *S. cuspidatum,* were the predominant semi-aquatic *Sphagnum* species pioneering the lake margin. *Sphagnum papillosum* frequently becomes more prominent in less saturated microhabitats (Vitt and Slack 1975), although along the lake margin at Little Dollar Lake (mean pH = 4.5, n = 40) *S. papillosum* grew both emergent above the water level, and partially submerged

Table 10. Mean percent cover and percent frequency of dominant and associated species in the *Sphagnum papillosum* phase of the *Chamaedaphne calyculata–Triadenum fraseri* cover type (10 quadrats). Species having less than 20% frequency are not included in the table. *TWINSPAN indicator species.

	Mean % Cover	% Frequency
BRYOPHYTES		
Sphagnum papillosum	49	80.0
Sphagnum magellanicum	9	40.0
Sphagnum cuspidatum	41	40.0
Sphagnum recurvum	5	20.0
Sphagnum capillifolium	10	20.0
VASCULAR PLANTS		
Chamaedaphne calyculata	47	90.0
Triadenum fraseri	4	80.0
Carex canescens	36	50.0
Vaccinium macrocarpon	10	50.0
*Carex lasiocarpa**	22	40.0
Sarracenia purpurea	4	40.0
Drosera rotundifolia	2	30.0
Eriocaulon aquaticum	3	30.0
Kalmia polifolia	3	30.0
Vaccinium oxycoccos	1	30.0
Rhynchospora alba	<1	20.0
Scheuchzeria palustris	5	20.0
Utricularia geminiscapa	<1	20.0

among *Chamaedaphne calyculata* branches in the lake (Hellquist 1996).

In northern Michigan, *Sphagnum papillosum* is known to inhabit wetter, more mineral rich habitats on mats or lake margins influenced by water movement (Crum 1983, 1988). In Ontario, *S. papillosum* is also associated with lake edge vegetation sequences (Vitt and Bayley 1984). The liverwort *Cladopodiella fluitans* also seems to indicate the acid nature of the lake margin community based on its preferred pH range of 3.7 to 5.0 (Gorham and Janssens 1992b). In Maine, sedge-moss lawn communities characterized by *S. papillosum, S. magellanicum, Carex limosa, Rhynchospora alba,* and *Scheuchzeria palustris* were found in "very acidic" to "moderately acidic" fens (Anderson and Davis 1997).

Vitt and Slack (1975) cite *Carex limosa* as being essentially restricted to this zone. At Little Dollar Lake, *C. limosa* was primarily found along the lake margin with the exception of a few scattered localities in wet areas of the *Calamagrostis canadensis* CT. Of the four species described as characteristic of this community by Vitt and Slack (1975), only *Carex paupercula* Michx. was absent at Little Dollar Lake.

4. *Potamogeton confervoides–Utricularia geminiscapa* Cover Type

The depauperate aquatic flora of Little Dollar Lake reflected the acidity of the lake water. The aquatic flora consisted of three submersed species (*Isoëtes echinospora* Durieu, *Utricularia geminiscapa,* and *Potamogeton confervoides*) and two floating species (*Nuphar variegata* Durand and *Nymphaea odorata* Aiton). Two submersed and/or emergent species, *Eriocaulon aquaticum* and *Hypericum boreale* (Britton) E. Bickn. forma *callitrichoides* Fassett, were also present in or along the lake (Hellquist 1996; Hellquist and Crow 1997).

Potamogeton confervoides and *Utricularia geminiscapa* were concentrated along the periphery of the floating mat, among the submerged rhizomes and roots of ericaceous shrubs growing into the open water of the lake. While *P. confervoides* was especially abundant and fruited copiously in the summer of 1994, it seemed less abundant in 1995, and was not fruiting as prolifically as in 1994. In 1996 the population continued to recede, with the majority of the population scattered along the lake margin of the eastern and southern mats. Previously, it had been found around the entire circumference of the lake.

In Michigan, *Potamogeton confervoides* occurs locally in lakes and acid bogs (Voss 1972) and is listed as a state of Michigan Threatened Species (Anonymous 1994; Beaman et al. 1985), although its status as Threatened may be due to under-collection rather than to actual rarity. In New England, *P. confervoides* is associated with soft waters, including high elevation ponds and lakes (Hellquist 1980). It is characteristic of extremely acidic waters with low alkalinity values (maximum alkalinity value 8.5 mg/l $CaCO_3$) and is the only pondweed found in *Sphagnum* bog ponds (Hellquist 1980).

Utricularia geminiscapa was also found submersed along the edge of the floating mat. In New England, *U. geminiscapa* is associated with bog ponds and acidic to moderately alkaline waters with a pH of 3.5–8.6 and alkalinity of 5.4–69.5 mg/l $CaCO_3$

(Crow and Hellquist 1985). Like *Potamogeton confervoides,* the abundance of *U. geminiscapa* was noticably lower in 1996 than in the two previous years.

Isoëtes echinospora grew submersed in the sandy sediments on the bottom of Little Dollar Lake. Individuals tended to grow widely scattered and were most conspicuous in shallow water off the eastern mat. In 1996, *Hypericum boreale* forma *callitrichoides,* an aquatic to partially emergent growth form, was thriving in the water along the edge of the eastern mat.

Evidence of terrestrialization and small-scale paludification processes at Little Dollar Lake. In an analysis of the pollen and sediment stratigraphy of Little Dollar Lake, Futyma (1982) stated that since the formation of the peatland approximately 3500 years before present, at least fifty percent of the surface area of Little Dollar Lake had been covered by peatland vegetation. At the time of this study, evidence of these terrestrialization patterns was visible at Little Dollar Lake in the former stream channel as well as in the muck pool area of the southern mat extension.

Apparent botanical evidence of terrestrialization was observed in the muck pools of the *Sphagnum cuspidatum–Dulichium arundinaceum* PHS of the *Calamagrostis canadensis* CT, and in the various areas of the *S. majus* and *S. papillosum* phases of the *Chamaedaphne calyculata–Triadenum fraseri* CT (Hellquist 1996). In these areas there was evidence from relict aquatic vegetation, as well as from aerial photography, that previously aquatic habitats were being colonized by emergent wetland vegetation (Hellquist 1996).

At Little Dollar Lake peatland, apparent on-going terrestrialization was most conspicuous at the muck pools in the southeastern lagg of the southern mat extension. These muck pools experienced conditions that vacillated between exposure and submergence. Along the edges of these mucky areas *Chamaedaphne calyculata, Carex lasiocarpa, Dulichium arundinaceum,* and *Glyceria canadensis,* as well as other emergent vascular species, were well established and were apparently encroaching into the open areas of peaty muck.

In 1994 and 1995, the muck pools contained stranded aquatic vascular plant species that were directly subjected to the fluctuating water levels of the peatland. One of the stranded aquatic species was *Potamogeton oakesianus* Robbins, which grew stunted and infertile with "floating" leaves lying on the surface of the mucky peat. Another stranded aquatic species, *Sparganium minimum* (Hartman) Fries, was found fruiting abundantly along the edges of the muck pools. *Utricularia intermedia* Hayne also grew in the peaty muck. In 1995, *U. intermedia* was extremely scarce with less than ten individuals located. However, when the muck pools were flooded in 1996, *U. intermedia* was frequent, with many lush, thriving individuals growing among the emergent vegetation.

There was also evidence of terrestrialization in the stream channel that wound through the southern mat and southern mat extension. The intermittently aquatic stream channel was colonized by a tenuous, loose network of *Carex lasiocarpa* that readily sank and quaked extensively when walked upon. This channel was also home to approximately 25 emergent clusters of stranded *Nuphar variegata* that were surrounded entirely by *C. lasiocarpa* and scattered individuals of *Potentilla palustris* in an approximately 3.0 m × 3.0 m area (Hellquist 1996). In a 1978 infrared aerial photograph, this stream channel was visible as open water whereas 1995 aerial photos and concurrent ground surveys clearly showed that, although still visible, the channel had become entirely covered by a quaking mat of vegetation dominated by *C. lasiocarpa* (see Hellquist 1996 and Hellquist and Crow 1997 for photographs).

Water levels in 1994 and 1995 were relatively low, but in 1996 the stream channel and muck pool areas became partially submerged by high water levels. In most areas, the *Sphagnum majus* PHS was covered by water with a minimum depth of ca. 20 cm. Presumably during high water years, terrestrialization by emergent sedges and other wetland taxa such as *Potentilla palustris* probably does not progress as rapidly as in drier years. Therefore, if the peatland experiences more dry years than wet years, expansion of the sedge-dominated mat would continue, and peat deposition and plant colonization would further promote terrestrialization. This process could occur relatively rapidly in an area as confined as the stream channel.

A similar rapid terrestrialization process has occurred at Weber Lake Bog in Cheboygan County, Michigan. A small pool of open water fringed by *Carex lasiocarpa* was mapped by University of Michigan Biological Station ecology classes in 1967 (Vitt and Slack 1975). When examined by Vitt and Slack in the mid-1970s neither the open water nor *C. lasiocarpa* was present. The pool was replaced by an open mat community with stranded clumps of *Dulichium arundinaceum.* During the summer of 1995, the area that had once been open water was still apparent, and contained stranded individuals of *Nuphar variegata,* as well as a few isolated individuals of *C. limosa. Carex lasiocarpa* has remained absent at Weber Lake Bog (E. G. Voss and C. E. Hellquist, pers. obs. 1995).

In some lagg areas of the *Iris versicolor–Lycopus uniflorus* PHS at Little Dollar Lake, small-scale paludification was observed where *Sphagnum* spp. were growing onto upland slopes. The process of paludification often is associated with rising water levels, especially in shallow, flat basins (Crum 1988). In some basin peatlands in northern Michigan, paludification is initiated by the compression of the lowermost peat layers. These compacted layers become so tightly condensed that they act as a sealant that prevents water from percolating out of the basin. Thus, any water entering the basin is retained by the more porous upper peat layers (Futyma 1982). This sequence is believed to have resulted in paludification at other Michigan peatlands, including Tahquamenon Bog and the Trout Lake peatlands in Chippewa County (Futyma 1982) and Lake Sixteen peatland in Cheboygan County (Futyma and Miller 1986). At Little Dollar Lake, the gradual creep of *Sphagnum* onto upland soils in some areas can probably be attributed to pooling of water trapped in the lagg.

Based on pollen and stratigraphic analysis from Futyma (1982), as well as field and photographic evidence described by Hellquist (1996) and Hellquist and Crow (1997) there seems to be satisfactory botanical evidence illustrating terrestrialization and paludification processes at Little Dollar Lake peatland. The patterns observed follow the "bog climax model" of peatland succession proposed by Klinger (1996), where areas of water are colonized by extensive, but irregular growth of vegetation while paludification proceeds as peat is deposited over upland soils along the margin of the bog basin. At Little Dollar Lake the areas along the lakeshore, stream channel, and muck pools with stranded aquatic taxa seem to be indicative of terrestrialization processes whereas paludification is less easily discerned, but still present in some lagg areas.

Little Dollar Lake peatland classification. The majority of northern Michigan peatlands exist in glacial topography and remain under the influence of local hydrology. Despite the fact that most of these peatlands are dominated by *Sphagnum*, they are best classified as fens (Vitt et al. 1975). Little Dollar Lake corresponds well to the delineation of a northern Michigan poor fen or "bog" (i.e. a more acid, oligotrophic peatland) as defined by Schwintzer (1981). Schwintzer (1981) states that these peatlands are weakly minerotrophic with low pH values (3.8–4.3) and low concentrations of calcium cations (1.2–3.7 mg/L). These poor fen complexes have a prominent *Sphagnum* cover, low vascular species richness, well developed open areas dominated by ericaceous shrubs, and reduced tree cover (Schwintzer 1981).

This study and its companion studies (Hellquist 1996; Hellquist and Crow 1997) have documented the flora and described the vegetation patterns within Little Dollar Lake peatland. This analysis, used in conjunction with the postglacial history of the Little Dollar Lake basin (Futyma 1982), has laid a foundation for subsequent studies that may further elucidate the dynamic processes (e.g., hydrology, nutrient regimes, interspecific plant interactions, plant-herbivore interactions, successional patterns) that influence the abundance and distribution of peatland vegetation at Little Dollar Lake.

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